

applicable to the solution of stratigraphic problems. The reason for this backwardness lies neither in the lack of good material (in the field) nor in the availability of equipment required for such studies, but principally in the failure of geologically-biologically educated students and acceptable materials to meet under favorable auspices. Both the geologist and the plant-anatomist are in part to blame for this state of affairs—the geologist for collecting uncritically and the anatomist for rejecting the poor material with unconcealed disdain—the whole performance resulting in general discouragement. It is hoped, however, that this unfortunate impasse can presently be overcome and that all good specimens of *Tempskya*, fossil wood, and other plant petrifications may receive adequate attention. The collector should be advised that acceptable collecting will be seasoned with discrimination and will provide representative specimens, not necessarily bulky, but showing the essentials required for identification, such as the stems in *Tempskya*, the central core or pith in gymnosperms and angiosperms, as the case may be, and a generous portion of the best development of the wood. Thus, because fossil wood usually occurs as broken trunks or stumps of such large size as to dismay the uninformed collector, it becomes a matter of exercising nicety of judgment in selecting, with the help of a hand lens, only typical portions that have well-preserved features of diagnostic value.

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ZOOLOGY.—*The histology of nemic esophagi*. V. *The esophagi of Rhabditis, Anguillulina, and Aphelenchus*.¹ B. G. CHITWOOD, Bureau of Animal Industry, and M. B. CHITWOOD.

This is the fifth paper of a series dealing with the structure of the esophagi of various groups of nematodes. In the previous papers (Chitwood and Chitwood, 1934-1935) the histology of the esophagi of *Rhabdias eustreptos*, *Oesophagostomum dentatum*, *Heterakis gallinae*, and *Metestrongylus elongatus* has been described. The nomenclature in this paper is the same as that used in previous ones.

¹ Received March 13, 1935.

In the present paper, the esophagi of *Rhabditis terricola* and *R. lambdiensis* are described in full, while descriptions of the esophagi of *Anguillulina dipsaci* and *Aphelenchus avenae* are given in brief and in the form of a comparison with those of the species of *Rhabditis*.

THE ESOPHAGI OF RHABDITIS TERRICOLA AND R. LAMBDIENSIS

Both of these species were studied in detail, the results being nearly, but not entirely, identical. The description is based on *R. terricola*, comparisons with *R. lambdiensis* being made where differences were noted. Illustrations were made of the species of which the best sections were available.

GROSS MORPHOLOGY. The esophagus of *Rhabditis terricola* is 144 to 172 μ long and consists of 3 major parts: A corpus distinctly subdivided into an anterior part, the precorpus, 58 to 70 μ long, and a posterior part, the postcorpus, 24 to 34 μ long; an isthmus 30 to 42 μ long; and a bulb 30 μ long. The precorpus is cylindrical, some of its tissue extending anteriorly and surrounding the mesostom and telostom. The lumen of the precorpus is somewhat subtriangular at the base of the stoma; immediately posterior to this point it becomes triradiate, each radius terminating distally in a small, incomplete "tube." In *R. lambdiensis* these "tubes" are much larger than in *R. terricola*. The "tubes" gradually become smaller in the posterior part of the precorpus and disappear in the postcorpus. The postcorpus takes the shape of a fusiform swelling commonly called the "median bulb"; its lumen is triradiate, the walls of the radii converging distally. The isthmus is a long, narrow region, the lumen being similar to that of the precorpus. The bulb is pyriform and contains a well developed valvular apparatus which alters the shape of the lumen. The cuticle lining the anterior part of the value is relatively thin, the lumen subtriangular to triradiate according to the stage of contraction. This is followed by the esophageal valve which consists of thickened parts of the cuticular lining to which muscles are attached.

NUCLEAR DISTRIBUTION. *Precorpus.* There are 18 nuclei in the precorpus of which 12 are of nerve cells (n_{1-12}) and 6 are of the radial muscle fibers (r_{1-6}). The nerve cell nuclei are arranged in 4 groups of 3 nuclei each, 1 nucleus being in the center of each esophageal sector. The first group (n_{1-3}) is situated a short distance from the anterior end of the corpus; the second, third, and fourth groups (n_{4-6} , n_{7-9} , and n_{11-12}) are situated in series, one behind the other. The radial nuclei (r_{1-6}) are arranged as a single group of 6 nuclei, 1 on each side of each esophageal sector, the group being situated near the base of the precorpus and between the third and fourth groups of nerve cell nuclei. In *Rhabditis lambdiensis* the same number of nuclei are present as in *R. terricola*, but the fourth group of nerve cell nuclei (n_{11-12}) is situated anterior to the radial nuclei (r_{1-6}).

Postcorpus. There are 28 nuclei in the postcorpus, comprising 6 radial

nuclei (r_{7-12}), 3 marginal nuclei (m_{1-3}), and 19 nerve cell nuclei (n_{13-31}). The marginal nuclei are situated near the anterior end of the postcorpus, 1 at the end of each esophageal radius; these nuclei are usually bilobed, the lobes being designated *a* and *b* (see m_{1a} , etc., in Fig. 1). This lobing of m_{1-3} is discussed in the description of the nuclei. The radial nuclei (r_{7-12}) are situated near the middle of the postcorpus and arranged as in the case of the first group (r_{1-6}). The nuclei of the nerve cells are arranged as a chain in the dorsal sector ($n_{13,16,23,28,29}$) and similarly in each subventral sector ($n_{14,17,19,21,24,26,30}$ and $n_{15,18,20,22,25,27,31}$). The nuclei in each sector are situated near the center of the sector, but the distance from the lumen varies considerably; for the

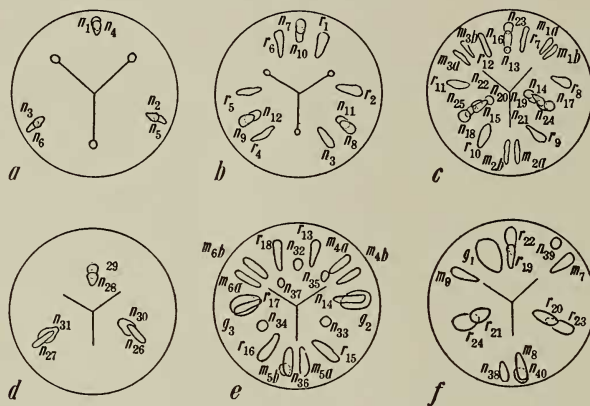


Fig. 1.—*Rhabditis terricola*; diagrammatic representation of the esophagus, a-b, precorpus; c-d, postcorpus; e-f, bulb.

relative positions see Figs. 1-2. The 3 most posterior nerve cell nuclei (n_{29-31}) are situated just posterior to the orifices of the subventral esophageal glands 1 being external to each of the 3 gland masses.

Isthmus. No nuclei are present.

Prevalvar region. The prevalvar and valvar regions of the esophagus are not distinctly separate. Contraction of the valve changes the relative positions of nuclei and for that reason the nuclei of the valvar region are included with those of the prevalvar region. There are a total of 17 nuclei in this region as follows: 6 radial nuclei (r_{13-18}), 3 bilobed marginal nuclei (m_{4-6}), 6 nerve cell nuclei (n_{32-37}), and 2 gland cell nuclei (g_{2-3}). The marginal nuclei are situated near the anterior end of the prevalvar region at the ends of the esophageal radii, 1 lobe lying on each side of each radius (Fig. 1). The radial muscle nuclei (r_{13-18}) are situated 4 to 10μ posterior to the marginal nuclei, 1 on each side of each sector. These nuclei are nearer the center of their sectors than those of the previous radial nuclei (r_{1-6} and r_{7-12}). The nerve cell nuclei n_{32-34} are situated near the posterior level of the radial nuclei, 1 in the center of each sector. The nerve cell nuclei n_{35-37} are situated 4 to 6μ posterior to n_{32-34} , 1 on each side of the dorsal sector, n_{35} being near the lumen at the

right side and n_{37} near the margin of the sector on the left side. The gland nuclei (g_{2-3}) are in the lateral parts of the subventral sectors or sometimes in the lateral parts of the dorsal sector; their position may be at the posterior level of the radial nuclei (Fig. 1) or at the level of n_{37} .

Postvalvar region. The postvalvar region contains 13 nuclei as follows 6 radial nuclei (r_{19-24}), 3 marginal nuclei (m_{7-9}), 3 nerve cell nuclei (n_{38-40}), and 1 gland nucleus (g_1). The radial nuclei are arranged in 2 groups of 3 nuclei each (r_{19-21} and r_{22-24}), 1 nucleus in the center of each sector, the first group being 3 to 6 μ anterior to the second group and nearer the lumen than the second group (Fig. 2). The marginal nuclei (m_{7-9}) are arranged as a single

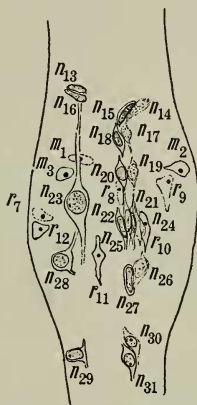


Fig. 2.—*R. lambdiensis*; longitudinal reconstruction of postcorpus.

group, 1 nucleus being at the side of each esophageal radius; their relative position varies considerably. The nerve cell nucleus n_{38} is situated on the right side of the ventral esophageal radius, whereas n_{40} is situated on the left side of the same radius and n_{39} on the dorsal side of the left subdorsal radius. The gland cell nucleus g_1 is near the posterior end of the postvalvar region on the right side of the dorsal sector.

ESOPHAGO-INTESTINAL VALVE. The esophago-intestinal valve is comparatively large and well developed in *Rhabditis* and consists of a trilobed internal structure and a circular external structure. Seven nuclei have been observed in these structures, but it is difficult to determine with certainty which nuclei belong to each of the two parts. Their positions vary somewhat, but usually there are 2 subdorsal nuclei, 2 dorsolateral or lateral nuclei, 2 subventral nuclei, and 1 ventral nucleus.

CHARACTER OF NUCLEI. The radial nuclei each contain 1 nucleolus or sometimes 2 nucleoli, moderately large in either case, surrounded by a nucleoplasm having little or no affinity for stains. The radial nuclei of the first group (r_{1-6}) are oval in cross section, (Fig. 3a); they are very much compressed longitudinally and often quite long. The radial nuclei of the second group (r_{7-12}) are similar to those of the first group in being oval in cross sec-

tion (Fig. 3b), but they may not be quite as elongate longitudinally (Fig. 2). The radial nuclei of the third group (r_{13-18}) are less oval in cross section (Fig. 3c), and not elongated longitudinally; there is considerable irregularity in shape. The radial nuclei of the fourth group (r_{19-21}) are nearly spherical and rest in a densely staining cytoplasm (Fig. 3e) which appears to be very similar to the cytoplasm of the esophageal glands. The radial nuclei of the fifth group (r_{22-24}) are usually somewhat compressed (Fig. 3f), their shapes depending on the state of contraction of their associated muscles.

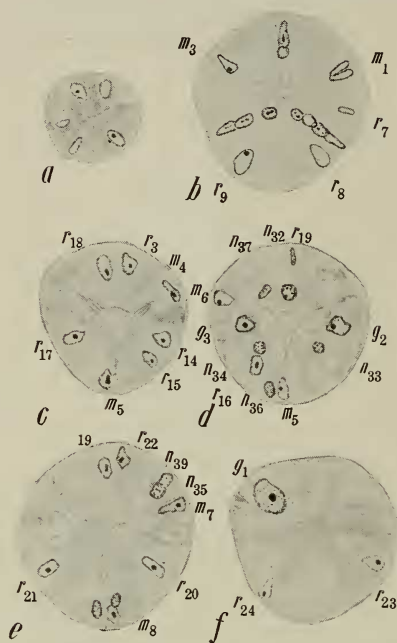


Fig. 3.—*R. terricola*; cross sections of the esophagus. a, precorpus at level of n_{1-6} ; b, postcorpus, compare with Fig. 1a; *R. lambdiensis* c-f, bulb (serial sections).

The marginal nuclei are similar to the radials in that the nucleoplasm has little or no affinity for stain and each nucleus contains 1 or 2 nucleoli. The marginal nuclei of the first and second groups ($m_{1-3,4-6}$) are usually bilobed, each lobe containing a nucleolus. The lobes are joined anteriorly (Fig. 3 b-d). The third group of marginal nuclei (m_{7-9}) are similar in character to those of the second groups but not lobed (Fig. 3e). The nuclei of the first and second groups of marginals are apparently not lobed in *Rhabditis lambdiensis* (Fig. 2).

The nuclei of the esophageal glands (g_{1-3}) are larger than other nuclei of the esophagus with the exception of the nuclei of the fourth group of radials (r_{19-21}); they are generally similar to r_{19-21} being somewhat spherical and having 2 large nucleoli. The dorsal esophageal gland nucleus (g_1) is the largest nucleus of the esophagus (Fig. 3f), while the subventral nuclei (g_{2-3})

are of about the same size as the radial nuclei (r_{19-21}) (Fig. 3d). The nucleoplasm contains a few coarse basophilic granules and there is often a dense basophilic margin adjacent to the inconspicuous nuclear membrane.

The nuclei of the nerve cells of the esophagus differ from the other nuclei in that the nucleoplasm has a very definite affinity for basic stains. The basophilic material is concentrated next to the nuclear membrane for the most part, but clumps of granular material are present also near the center of the nucleus. Nucleoli were not always observed in the nerve cells but quite often a bilobed nucleolus was seen. The nerve cell nuclei are spherical or slightly elongated, and are so consistent in appearance that they may be easily recognized by reference to Figures 2 and 3. The protoplasm surrounding the nerve cell nuclei is relatively meager and no particular study of it was made. The neurones of the precorpus (n_{1-12}) all appear to be bipolar, as do all except 3 (n_{26-28}) of the postcorpus (Fig. 2). The exceptions (n_{26-28}) are neurones of the commissure which is situated in the posterior part of the postcorpus. The nerve cells which are situated posterior to n_{29-31} may be commissural cells also. The nerve cells of the preavalvar region (n_{32-36}) are commissural cells of the preavalvar and avalvar region, while the remaining nerve cell of this region (n_{37}) and those of the postavalvar region (n_{38-40}) are probably a part of a postavalvar commissure; the later commissure has not been observed with certainty.

ESOPHAGEAL GLANDS. There are 3 esophageal glands, 1 dorsal and 2 subventral. The dorsal gland opens at the base of the glottoid apparatus through a very short transverse duct lined with cuticle. This duct dilates distally from the orifice, forming an ampulla which may or may not be lined with cuticle (facts uncertain). A narrow tube not lined with cuticle extends posteriorly from the ampulla through the middle of the dorsal sector. In the precorpus this tube is surrounded by a very meager amount of glandular protoplasm. In the postcorpus the glandular mass becomes a little larger and branches from the tube have been observed, and in the isthmus the glandular mass is represented only by a delicate strand of protoplasm. The dorsal gland becomes larger and lobed posterior to the valve and is most concentrated in the right side of the dorsal sector where its nucleus lies. The glandular protoplasm at the level of the nucleus is reticulate or facuolate.

The subventral esophageal glands open into the lumen of the esophagus near the base of the corpus, between the levels of the nerve cell nuclei n_{26-28} and n_{29-31} . Like the dorsal gland, each has a short transverse duct lined with cuticle which is connected with an ampulla; the protoplasm of the gland is rather extensive and reticulate in this region, the reticuli being apparently in direct communication with the lumen of the ampulla. The subventral gland masses become narrow and strand-like in the isthmus and remain of this character in the anterior part of the preavalvar region. In the posterior part of the preavalvar region and in the avalvar region the gland masses are multilobed and reticulate.

THE ESOPHAGUS OF *ANGUILLULINA DIPSACI*

The esophagus of *Anguillulina dipsaci* (Fig. 4) consists of the same general regions as the esophagus of *Rhabditis*, but differs in that the corpus and isthmus are proportionately thinner, and the bulbar region is cylindroid

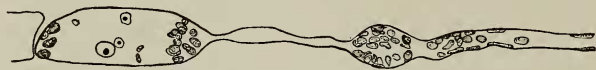


Fig. 4.—*Anguillulina dipsaci*; longitudinal reconstruction of esophagus.

instead of pyriform and is entirely devoid of valves. This type of posterior swelling has been termed a pseudobulb although it is homologous with the bulb of *Rhabditis*. The lumen of the entire esophagus is greatly reduced (Fig. 5), being scarcely distinguishable except in the postcorpus (Fig. 5).

The precorpus apparently contains either 15 or 18 nuclei the arrangement and nature of which were not determined. The postcorpus contains 25 nuclei (Fig. 5) which appear to consist of 2 sets of radial nuclei (r_{1-6} , r_{7-12}), 1 set of marginal nuclei (m_{1-3}), and 10 nerve cell nuclei (n_{1-10}). These designations, it should be noted, were made on the basis of comparison with *Rhabditis* and not on purely structural grounds. The isthmus is exceedingly minute in cross

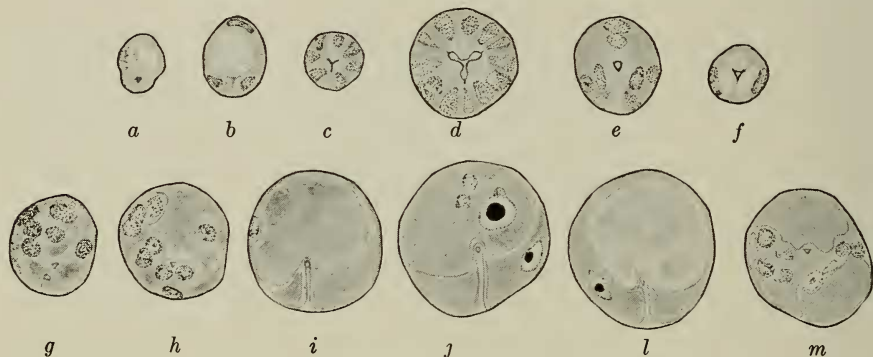


Fig. 5.—*A. dipsaci*; cross sections of esophagus. a-b, precorpus; c-f, postcorpus (serial sections); g-m, bulbar region (serial sections).

section and, like other forms, contains no nuclei. The bulbar region is most interesting, for although 30 nuclei have been found as in *Rhabditis*, there is practically no similarity in other respects. The musculature is exceedingly degenerate, and the esophageal gland tissue massive. Small nuclei are grouped near the anterior and posterior ends of the bulbar region (Fig. 5) with no apparent symmetry. The dorsal and subventral esophageal gland nuclei stand out in contrast, being of much greater size than the other nuclei. As shown by Goodey (1929), the dorsal esophageal gland opens into the esophagus at the base of the stylet and the subventrals open at the base of the postcorpus.

THE ESOPHAGUS OF APHELENCHUS AVENAE

The esophagus of *Aphelenchus avenae* is similar to that of *Anguillulina* with several outstanding exceptions, the most conspicuous being the more massive development of the postcorpus and the degeneration of the bulbar region, the latter feature allowing the esophageal glands to lie in the body cavity. We find but 10 nuclei in the precorpus and 33 in the postcorpus (Fig. 6), the total number being the same as in *Anguillulina*. Of the 33 nuclei in the postcorpus, 15 (r_{1-12} , m_{1-3}) appear to check with those in *Anguillulina*, but the different arrangement of the remaining 18 nuclei makes their recognition impractical. The bulbar region appears to have 30 nuclei arranged without apparent symmetry (Fig. 6). Only the 3 esophageal gland nuclei

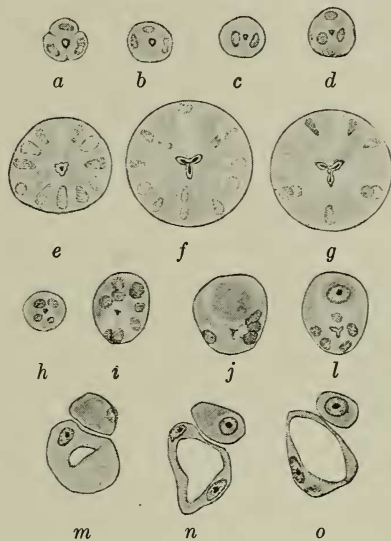


Fig. 6.—*Aphelenchus avenae*; cross sections of esophagus. a-d, precorpus; e-g, postcorpus; h-o, bulbar region.

are clearly recognizable. One point is notable, namely, that the esophageal glands, which extend posteriorly as a cylindroid mass of tissue, are surrounded by a nucleated covering. The fibrous tissue corresponding to these nuclei probably represents marginal or radial fibers. Goodey (1929) found that the dorsal esophageal gland opens in the anterior part of the postcorpus, whereas the subventrals open in the usual position; the writers were not able to verify or disprove this observation, but on the basis of sections it appears probable that he is correct.

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